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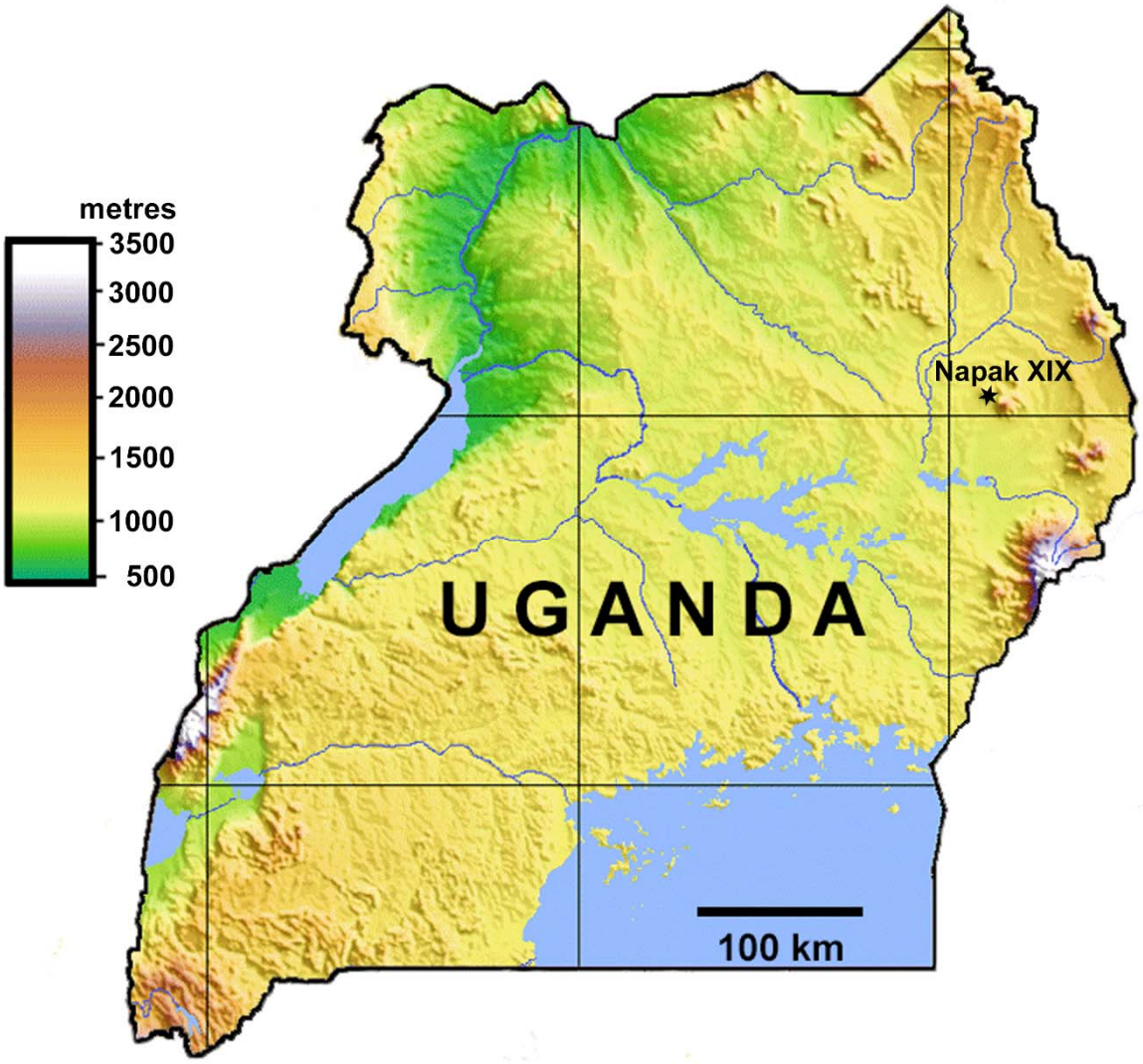

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Geo-Pal Uganda

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5 Production

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The lower permanent dental formula of *Rusingameryx aequatorialis* (Bothriodontinae, Anthracotheriidae), early Miocene, Africa

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ABSTRACT

The recovery of an almost complete mandible of *Rusingameryx aequatorialis* at locality Napak XIX (Iriri Member, ca 20 +/- 0.5 Ma) clarifies the permanent lower dental formula of large early Miocene bothriodonts, a subject about which there has been debate in the literature. Even though the specimen is slightly crushed and cracked, much of the anatomy can be ascertained reasonably well. Three tooth are missing entirely (only their alveoli are preserved) and four teeth are represented by their roots, which means that the entire adult dental formula can be deduced (three incisors, one canine, four premolars and three molars in each hemimandible). The large tooth in the antero-lateral corner of the symphysis is the i/2 and not the i/3 or the canine as has on occasion been evoked in the literature.

Key words.- Bothriodontinae, Early Miocene, Uganda, Dental formula

INTRODUCTION

Pickford (2020a) pointed out that there has been a great deal of uncertainty about the meristic position of the anterior lower teeth of *Brachyodus* and closely related genera of large bothriodont anthracotheres. Several lineages suppressed one or more of the incisors and/or the canine, and developed diastemata between teeth. In most of the known lineages, however, the tooth in the antero-lateral corner of the symphysis is relatively enlarged, being the largest of the incisor/canine ensemble. Furthermore, there is marked sexual dimorphism and bimodality in this tooth, some male examples being hyper-developed, and thereby resembling the canines of other mammals.

For these reasons, some authors have inferred that the large tooth in the antero-lateral corner of the symphysis was the canine (Miller *et al*. 2014) whereas others hesitated between i/2 or i/3 and the canines (Fourtau, 1918; Dineur & Ginsburg, 1986; Ginsburg & Chevrier, 2005) (for a detailed discussion of this issue, see Pickford, 2020a). Among the authors who correctly concluded that the large tooth is the i/2, are Black (1978) and Cabard *et al.* (1980).

The 2022 field survey of the Uganda Palaeontology Expedition was notable for the discovery *in situ* of an almost complete mandible of *Rusingameryx aequatorialis* at locality NAP XIX in the basal sediments of the Iriri Member, aged ca 20 Ma. The specimen is cracked, slightly crushed and distorted, but retains 15 complete teeth. Of the missing teeth, four are represented by their roots and three by their alveoli. In each hemimandible, the teeth present comprise three incisors, a canine, four premolars and three molars, with a diastema ca 6 cm long between the canine and the first premolar.

MATERIAL AND METHODS

The fossil described herein is the greater part of a mandible from Napak XIX (02°06’10.37’’N - 34°13’19.69’’E), a locality in the basal sediments (Iriri Member) of Napak Palaeovolcano (early Miocene, ca 20 Ma). The specimen was found *in situ* in poorly consolidated purple sand/silt with small pedogenic carbonate concretions, some of

which were adhering to the fossil. The specimen is curated at the Uganda Museums, Kampala, under the catalogue number UM NAP XIX 1'22.

The terminology of teeth was defined in Pickford (2020a, 2020b).

Preparation

The mandible was extracted in a block of sediment which was transported to base camp (Fig. 1) and then cleaned of loose matrix (Fig. 2). The specimen comprises four main segments which were slightly separated in the sediments, one of which had already eroded out of place and had been transported a few metres downstream from the outcrop. The ensemble was then exported on loan to Paris where the carbonate concretions adhering to the bone were removed using a micro-graveur, the four pieces were stuck together using super-glue, and gaps in the bones infilled with Plaster-of-Paris (Fig. 3). Wooden struts have been added to the ventral part of the mandible in order to strengthen it.

Figure 1. Anthracothere mandible *in situ* in purple sand-silt deposits of the Iriri Member at locality Napak XIX, as exposed naturally, then being excavated and transported back to camp by Madalena Adiaka. The missing angle of the jaw was found several metres downstream of the outcrop (Photos B. Senut).

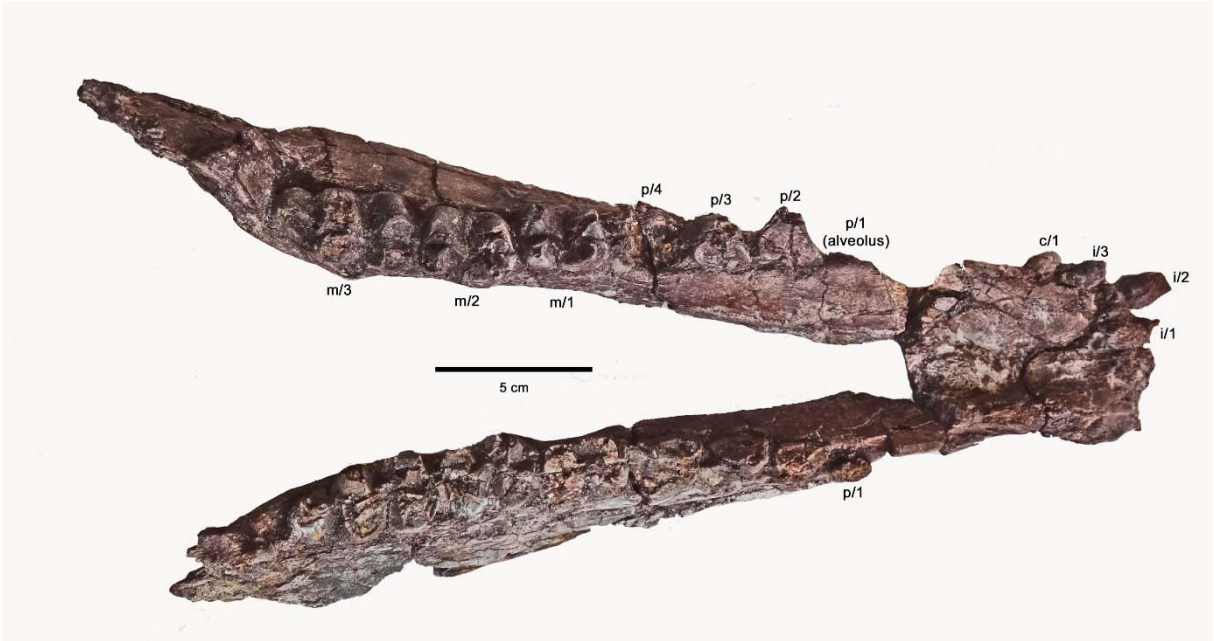

Figure 2. Dorsal view of mandible UM NAP XIX 1'22, *Rusingameryx aequatorialis*, after partial cleaning and reassembly in the field.

Comparative base

The mandible from Nap XIX has been compared with specimens of *Brachyodus onoideus*, *Brachyodus intermedius*, *Brachyodus depereti* and *Rusingameryx aequatorialis*. The Napak specimen accords most closely with a mandible from Rusinga Island, Kenya (KNM RU 1014; Black, 1978) attributed to *Rusingameryx aequatorialis* and is accordingly identified as such.

ASSOCIATED FAUNA AND FLORA

The sedimentary deposits at Napak XIX yield oncolites of algal origin as well as abundant bivalves and a few freshwater snails. The bivalves (*Pleiodon*) are often preserved as doublets indicating little or no post-mortem disturbance. The same deposits have yielded a polypterid fish, abundant crocodile teeth and scutes and freshwater chelonians. Among the large mammals found at the site, there are bunodont proboscideans, a brachypothere rhinocerotid and a large anthracothere. Medium-sized and small mammals are rare, but a ruminant and an orycteropodid (*Eteketoni platycephalus* Pickford, 2019) are known. Terrestrial snails are also represented (*Tholachatina*, *Burtoa*, *Tayloria*, Subulinidae) and there are fragments of fossil wood and insects are represented by termite fungus gardens, moth cocoons and fragments of millipede exoskeletons.

The sediments are thus inferred to have accumulated in a fluvio-palustral depositional environment with dry land close by.

SYSTEMATIC DESCRIPTION

Family Anthracotheriidae Leidy, 1869

Genus *Rusingameryx* Pickford, 2022

Species *Rusingameryx aequatorialis* (MacInnes, 1951)

Holotype.- KNM RU 1009, skull lacking the anterior parts of the premaxillae (curated at the Kenya National Museum, Nairobi).

Diagnosis and synonymy.- see Pickford, 2022.

Type locality and age.- Rusinga Island, Kenya, early Miocene, ca 18 Ma.

Description

The mandible is cracked and has suffered some distortion of the bones and teeth due to compression within the sediments. Nevertheless, the overall shape of the specimen can be reasonably reconstructed (Figs 2, 3). The right ascending ramus is missing, but the one on the left is mostly preserved but lacks part of the anterior margin and the coronoid process. The root of the mandibular condyle is dorso-ventrally compressed, the condyle itself being a hemi-cylinder, projecting medially from its base.

The symphysis is elongated and slightly klinognathic, the incisor alveolae being lower than the alveolar margins of the cheek teeth (Fig. 3A). The distal end of the symphysis is slightly anterior to the p/1 and there is a long diastema between the p/1 and the canine (Table 1). The ventral surface of the symphysis has two large foramina close to the sagittal plane and two smaller ones distally and somewhat distanced from the midline. The two foramina on the right side are joined by a groove, but those on the left are distinct from each other (partly infilled with Plaster-of-Paris) (Fig. 4).

The ascending ramus rises sharply immediately posterior to the m/3, thereby leaving room for only an extremely short retro-molar space. The base of the mandible shows a slight inflection beneath the rear of the m/3, but the descending angle is weakly expressed. Overall, the mandible is shallow but moderately robust.

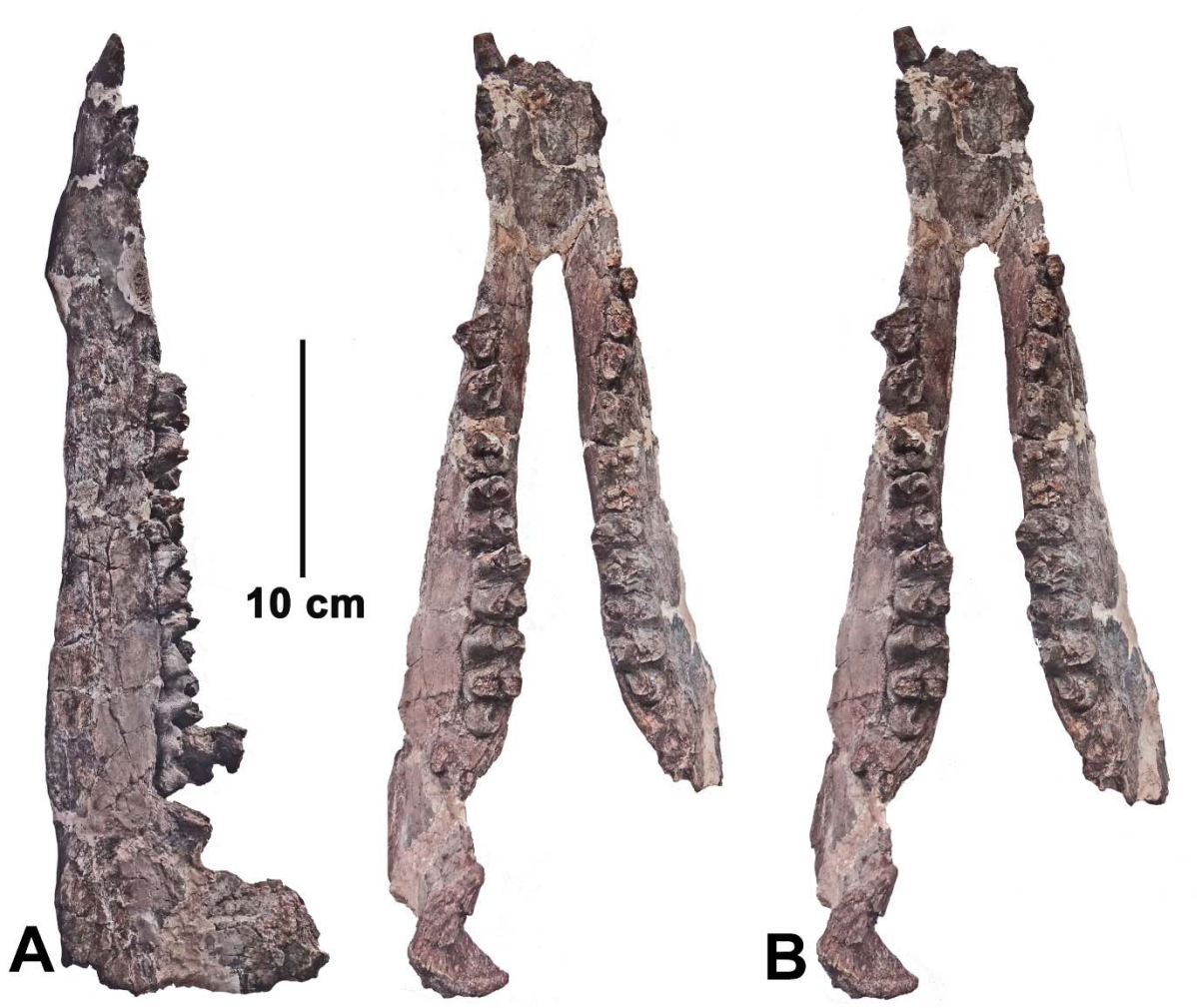

Figure 3. UM NAP XIX 1'22, mandible of *Rusingameryx aequatorialis* from Napak, Uganda. A) left lateral view, B) stereo occlusal view.

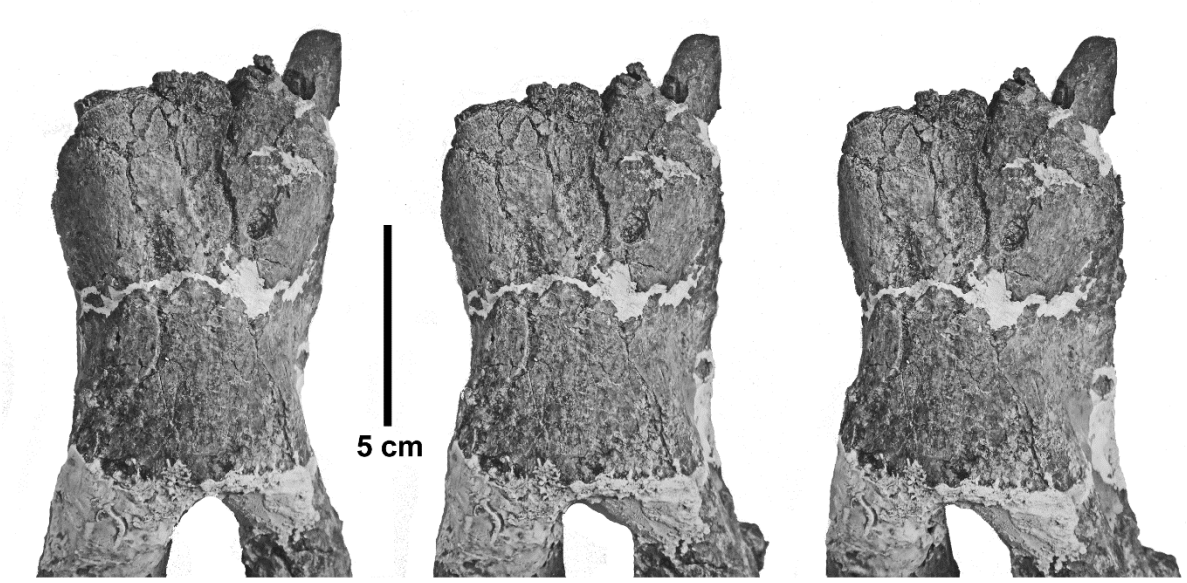

Figure 4. UM NAP XIX 1'22, mandible of *Rusingameryx aequatorialis* from Napak, Uganda. Stereo ventral views of the symphysis.

The left tooth row is the more complete, lacking only the crowns of the i/1 and the p/1. The i/1 is represented by its root which is small and of circular outline. The i/2 is the largest of the incisors (Table 2), but damage to the crown prevents a detailed description from being written. The i/3 and lower canine are small teeth of simple construction, but the state of preservation is poor. The crowns are labio-lingually compressed and appear to be comprised of a single cusp posed on a single root.

There is an elongated diastema between the c/1 and p/1 (Table 1).

The p/1, preserved only on the right side, is damaged and displaced laterally. The p/2 has a tall main cusp, from the apex of which sharp pre- and post-cristids descend towards the mesio-lingual and disto-lingual corners of the crown respectively, where they join a sharp and continuous lingual cingulum. It has two roots. The p/3 is basically an enlarged and broader version of the p/2. The p/4 is poorly preserved.

Table 1. Measurements (in mm) of the mandible of *Rusingameryx aequatorialis* UM NAP XIX 1'22.

Anatomy	**Dimensions**
Length of symphysis in mid-line	86
Breadth of symphysis at c/1	61
Depth of mandible at m/2	47.8e
Breadth of mandible at m/2	34.8e
Depth of mandible at m/3	55.0
Breadth of mandible at m/3	36.5
Medio-lateral diameter of mandibular condyle	39
Antero-posterior diameter of mandibular condyle	17.5
c/1-p/1 diastema left side	60
c/1-p/1 diastema right side	60
Length p/1-p/4 left side	86
Length p/1-p/4 right side	85.5
Length m/1-m/3 left side	112.8
Length m/1-m/3 right side	114
Length p/1-m/3 left side	197.5
Length p/1-m/3 right side	200

Table 2. Measurements (in mm) of teeth of *Rusingameryx aequatorialis* from Napak XIX (e - estimated measurement).

Tooth	Mesio-distal length	Bucco-lingual breadth	Bucco-lingual breadth 2nd lophid
i/1 lt (root)	7.4	10.7	
i/2 lt	14.0	13.3	
i/2 rt (root)	13	12	
i/3 lt	10.6	--	
c/1 lt	11.0	9.0	
p/1 lt (alveolus)	12.5	7.5	
p/1 rt	16e	9.6	
p/2 lt	23.0	15.8	
p/2 rt	20.6	14.3	
p/3 lt	25.0	19.0	
p/3 rt	22.0	18.0	
p/4 lt (alveolus)	20	17.5	
p/4 rt	21.8	18.2e	
m/1 lt	33.8	21.1	22.8
m/1 rt	30	21	--
m/2 lt	36.5	24.4	23.8
m/2 rt	34.4	23.6	21.8
m/3 lt	48.5	26.6	24.5
m/3 rt	50	26.2	25.0

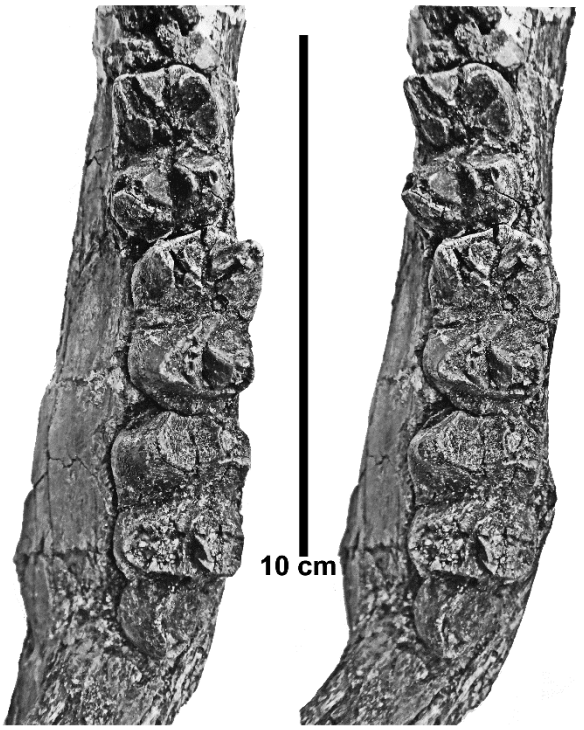

Figure 5. UM NAP XIX 1'22, mandible of *Rusingameryx aequatorialis* from Napak, Uganda. Stereo occlusal view of the left lower molar row.

The m/1 is quadricuspidate. The protoconid is tall and pointed and has sharp pre- and post-cristids which descend from its apex towards the midline of the crown, the precristid extending slightly beyond the midline to terminate opposite the apex of the metaconid. The metaconid has no precristid but the postcristid is well developed and is directed bucco-distally, approaching the postprotocristid at its base (Fig. 5). The lingual postmetacristid is sharp and is directed distally close to the lingual edge of the crown. The hypoconid has a strong precristid that descends mesio-lingually from its apex, terminating in a slight swelling opposite the apex of the entoconid, thereby forming a low barrier in the median transverse valley. The postmetacristid descends from the apex of the cusp disto-lingually towards the

midline of the crown, where it joins the postentocristid, thereby closing off the rear of the fovea between the hypoconid and entoconid. The distal cingulum is well formed, and has a distinct central cusplet (hypoconulid) in the midline of the crown. The mesial cingulum is preserved but is weakly developed.

The m/2 is an enlarged version of the m/1. The m/3 is pentacuspidate. The two anterior lophids are constructed along the same lines as the m/1 and m/2, but the hypoconulid is enlarged and elongated to the extent that it is almost as long as the protoconid. The hypoconulid has two cristids (prehypocristulid and posthypocristulid in the terminology of Lihoreau & Ducrocq, 2007) both of which are directed anteriorly, the precristulid terminating in the midline of the crown, and the postcristulid ending near the lingual edge of the posterior transverse valley.

DISCUSSION

Judging from the dimensions of the i/2, the Nap XIX anthracothere mandible represents a female individual. The klinognathic symphysis, the weakly descending angle, the shallow but thick ramus, the positions of the mental foramina, the relatively small symphyseal foramina, the strongly fused symphysis, and the elongated diastema between the canine and the p/1, all recall the genus *Rusingameryx* (see Black, 1978, figs 21.7 and 21.8). None of the previously available mandibles of this genus preserve the mandibular condyle, but its morphology and position in the specimen from Napak are similar to those observed in *Brachyodus depereti* from Moghara, Egypt (Fourtau, 1918).

The main cranio-dental differences between *Rusingameryx* and *Brachyodus* were enumerated by Pickford (2022). They relate to the platycephalic skull morphology of *Rusingameryx* which contrasts with the more hypsicephalic condition observed in *Brachyodus* (Pickford & MacLaren, 2022) The shallowness of the Napak mandible and its weakly descending angle correlate with the platycephalic state of the skull of *Rusingameryx*. Another difference between these genera is that *Brachyodus* shows a tendency to suppress the lower central incisor and the lower canine, as discussed by Black (1978, under the genus name *Masritherium*), but both of these teeth are present on both sides in the Napak mandible. In particular, Black (1978) mentioned that the lower canine might be absent in females of *Masritherium depereti* whereas it is present in the Napak jaw which is probably female on the basis of the dimensions of the i/2.

In a recent paper, Pickford (2020a) discussed the anthracothere material from Napak, based on fossils from the Napak Member of the palaeovolcanic succession. The Napak Member is younger than the Iriri Member, but the difference in age is not very great, the deposits being about 20 +/- 0.5 Ma. In that paper Pickford (2020a) some of the specimens were provisionally attributed to *Masritherium aequatorialis*, and others to an unknown genus and species morphometrically close to material from Thailand attributed to the genus *Brachyodus* by Ducrocq *et al*. (2003) The new specimen from the Iriri Member is morphometrically close to what was previously known as *Brachyodus aequatorialis* (or *Masritherium aequatorialis*) but recently placed in a distinct genus *Rusingameryx* by Pickford (2022) as the new combination *Rusingameryx aequatorialis*. The situation now is that the Napak anthracotheres belong to two taxa, *R. aequatoralis* and an unidentified species, possibly related to *Brachyodus*.

CONCLUSIONS

An almost complete mandible from early Miocene (20 +/- 0.5 Ma) sediments at Napak, Uganda, herein attributed to *Rusingameryx aequatorialis*, reveals that the lower dental formula of this species consisted of three incisors, a canine, four premolars and three molars. The premolars and molars form a continuous series of cheek teeth, separated from the canine by an elongated diastema. There is a short gap between the canine and the i/3. The i/2, situated at the antero-lateral corner of the fused symphysis, is the largest of the incisors. The dimensions of the i/2 in this mandible accord with female status.

The full eutherian dental formula in this mandible indicates that the enlarged tooth in the

antero-lateral corner of the mandible in bothriodont anthracotheres, is the second incisor, and not the i/3 or the canine, as has on occasion been postulated in the literature. As such the Napak discovery resolves the long-standing uncertainty about the lower dental formula or large bothriodont anthracotheres.

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